Seed losses due to spruce cone maggot, *Strobilomyia neanthracina* (Diptera: Anthomyiidae) in Newfoundland populations of white spruce, *Picea glauca,*(Moench) Voss.

A. Mosseler and P. Tricco

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SEED LOSSES DUE TO SPRUCE CONE MAGGOT, *STROBILOMYIA NEANTHRACINA* (DIPTERA: ANTHOMYIIDAE) IN NEWFOUNDLAND POPULATIONS OF WHITE SPRUCE, *PICEA GLAUCA* (MOENCH) VOSS.

by A. Mosseler and P. Tricco

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Abstract

Seed procurement has been insufficient to meet artificial regeneration requirements for the native spruces of Newfoundland. The effects of seed predation by the spruce cone maggot, *Strobilomyia neanthracina* Michelson, on seed yield and quality in natural populations and exotic provenances of white spruce, *Picea glauca* (Moench) Voss., were quantified to assess seed crop losses. No significant differences were observed in cone maggot incidence among 6 natural populations of white spruce, nor among exotic provenances from Ontario and Quebec that have been established in central Newfoundland. However, infestation levels were significantly higher in local populations of white spruce than in the mainland provenances, suggesting that these mainland seed sources may be less susceptible to infestation by the cone maggot. Only 4% of the total genetic variation in infestation level was attributable to provenance differences; the remainder was attributable to differences among trees within provenances. Similarly, in natural populations only about 4% of the total variation in infestation was due to differences among natural populations. Infestation by the spruce cone maggot resulted in an average reduction in number of full seeds/cone of 61%, indicating that the cone maggot is capable of causing important losses in seed production areas and seed orchards that are now being established in Newfoundland. The cone maggot may also have a significant impact on reproductive success in the small, isolated populations that characterize the distribution of white spruce in the centre of the Island.

Résumé

L'obtention de graines n'a pas suffi à répondre aux besoins de reboisement en essences indigènes d'épinettes à Terre-Neuve. Les effets de la déprédation de la mouche granivore de l'épinette, *Strobilomya neanthracina* Michelson, sur le rendement en semences et la qualité des graines des populations indigènes et des provenances exotiques d'épinette blanche, *Picea glauca* (Moench) Boss, ont été calculés afin d'évaluer le pourcentage de graines perdues. On n'a observé aucune différence significative de fréquence de la mouche granivore de l'épinette chez les épinettes blanches de six populations locales, ni chez celles introduites de l'Ontario et du Québec et implantées dans le centre de Terre-Neuve. Cependant, le degré d'infestation était significativement plus élevé chez les populations locales d'épinettes blanches que chez celles provenant du continent, ce qui donne à penser que ces dernières sources de semences sont moins vulnérables à l'infestation par la mouche granivore de l'épinette. Seulement 4 % de la variabilité génétique totale du degré d'infestation a été attribué à des différences entre les provenances; le reste l'a été à des différences entre les arbres de même provenance. Parallèlement, dans les populations naturelles, seulement 4 % de la variabilité totale a été attribuée à des différences entre ces populations. L'infestation par la mouche granivore de l'épinette a entraîné une réduction moyenne de 61 % du nombre de graines pleines par cône, ce qui indique que la mouche granivore est capable de causer des pertes importantes dans les zones de production de graines et les vergers à graines en voie d'implantation à Terre-Neuve. La mouche granivore de l'épinette peut aussi avoir de sérieuses répercussions sur l'aptitude à se régénérer des petites populations isolés caractéristiques de la distribution de l'épinette blanche dans le centre de l'île.

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SEED LOSSES DUE TO SPRUCE CONE MAGGOT, *STROBILOMYIA NEANTHRACINA* (DIPTERA: ANTHOMYIIDAE) IN NEWFOUNDLAND POPULATIONS OF WHITE SPRUCE, *PICEA GLAUCA* (MOENCH) VOSS.

Introduction

The spruce cone maggot, *Strobilomyia neanthracina* Michelson, is a major pest of white spruce, *Picea glauca* (Moench) Voss., cones, and is responsible for considerable seed losses (Tripp and Hedlin 1956; Werner 1964; Hedlin 1973; Turgeon 1990). The cone maggot has a transcontinental distribution in North America, and attacks all native spruces (Hedlin *et al.* 1981). Females lay their eggs between cone scales in the early stages of cone development, and the larva creates a spiral feeding tunnel around the cone axis, damaging cone scales and seeds, before exiting the cone in mid summer (Tripp 1952; Hedlin *et al.* 1981). Despite attempts to develop biological (Fogal 1986) and chemical (Hedlin 1973) control measures, no reliable control strategy exists for *S. neanthracina*.

Significant genetic variation in host susceptibility to cone pests has been observed in other tree species (Jenkins 1983; Askew *et al.* 1985), but there is little population-based information available on the susceptibility of white spruce to cone and seed predation by the cone maggot. Information on population variability, and genetic variation in susceptibility of white spruce to predation is needed to assess forest management options for the control of seed pests in seed orchards and seed production areas. Information on the impact of predation on reproductive success is also of ecological interest, particularly in marginal populations of a species at the limits of its geographic range. We quantified the effects of spruce cone maggot predation in Newfoundland populations of white spruce to assess seed losses, and determined the components of population variation in infestation and damage levels.

Materials and Methods

Cones were collected from 4 white spruce trees from each of 6 natural populations in central Newfoundland (Fig. 1) in 1988. A minimum of 200 mature cones from at least 5 different branches in the upper crown of each tree were harvested upon cone maturation. Similar cone samples were collected from 8 trees from each of 12 provenances originating from the Ontario and Quebec range of white spruce that were established in 1963 near Gambo, Newfoundland (Fig. 1; see Khalil (1985a) for the origins of these provenances) to study provenance or seed source variation in white spruce. To minimize the effects of tree size, we selected 12 provenances that showed no significant differences in growth performance (Hall 1986). Each cone sample was separated into 4 subgroups of 50 cones to count the number of cones with exit holes that identify spruce cone maggot infestation (Rose and Lindquist 1977). The cones were further partitioned into 3 samples: cones with no outward signs of insect damage, cones infested by the spruce cone maggot, and cones with other forms of insect feeding damage. The latter forms of damage were

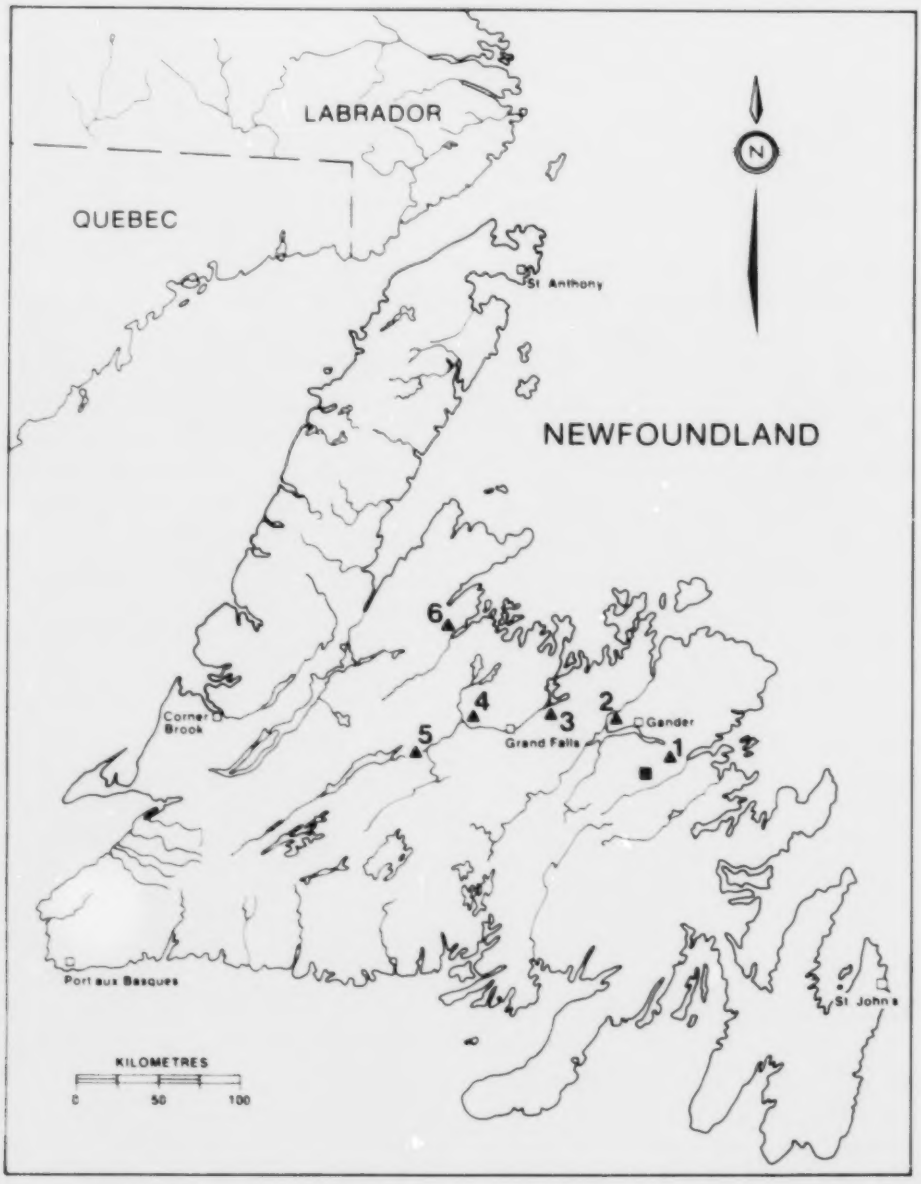

Figure 1. Origins of natural populations (▲) of white spruce in Newfoundland (Gambo - 1, Glenwood - 2, Norris Arm - 3, Badger - 4, Millertown - 5, and Springdale - 6), and site of provenances ( ) sampled for cone maggot infestation in 1988.

often attributable to unidentified lepidopterous species like *Dioryctria* sp. (Hedlin *et al.* 1981; West 1986).

Statistical analysis of the data on incidence of cone maggot in 4 samples of 50 cones per tree from 4 trees in 6 natural populations, and from 8 trees in 12 provenances of white spruce were based on the following ANOVA model:

$$Y_{ijk} = u + P_i + T_{(i)j} + \epsilon_{(ij)k},$$

where Y_{ijk} is the incidence of cone maggot (percent of cones infested) in the kth cone sample (k = 1...4), from the jth tree ($T_{(i)j}$, where j = 1...4, in trees from natural populations; and j = 1...8 in trees from the provenance test), nested within the ith natural population (P_i, where i = 1...6) or the ith provenance (P_i, where i = 1...12); u is the parametric mean of the population; and $\epsilon_{(ij)k}$ is the experimental error. Expected mean squares, and variance components (Table 1) were calculated as recommended by Anderson and McLean (1974) for a random effects model. All statistical analyses (DUNCAN, GLM, VARCOMP) and tests for normality (UNIVARIATE) were done with programs developed by the SAS Institute (1987).

ANOVA of cone and seed traits was based on 4 samples of 4 cones/sample/tree from 4 trees/population from each of 6 populations to assess variation in healthy or undamaged cones; cones with the exit holes of the spruce cone maggot; and cones with miscellaneous signs of insect feeding attributed to unidentified cone pests. Cones were allowed to open naturally in an unheated room following harvesting, and seeds were extracted by shaking them from cones. The following cone and seed parameters were determined based on a maximum of 4 samples of 4 cones/sample/tree: (i) the total number of seeds/cone, (ii) the number of filled and empty seeds/cone; (iii) seed weight; and (vi) cone weight. The ratio of empty seeds/cone to full seeds/cone was calculated. Seeds were counted with an electronic seed counter. Seeds were judged empty if they floated in 95% ethanol. The filled seed from each sample were weighed to the nearest 0.0001 g, and the seed weight per 1000 seeds was calculated. Cones per sample were weighed to the nearest 0.001 g following drying at 105°C for 24 hours.

Data on cone and seed traits from natural populations, were analysed by ANOVA according to the following model describing the components of variation:

$$Y_{ijkl} = u + P_i + T_{(i)j} + D_k + PD_{ik} + TD_{(i)jk} + \epsilon_{(ijk)l};$$

where, Y_{ijkl} is the effect on seed quality traits in the lth cone sample (l = 1...4) of the kth infestation level (D_k, where k = 1...3) from the jth tree ($T_{(i)j}$, where j = 1...4) nested within the ith natural population (P_i, where i = 1...6); u is the parametric population mean; and $\epsilon_{(ijk)l}$ is the experimental error. This is a mixed model in which provenances and trees are considered as random effects, and infestation level as a fixed effect for calculating the expected mean squares (Table 2).

Table 1. ANOVA for infestation levels of the spruce cone maggot during 1988 in natural populations of white spruce in Newfoundland, and in a group of provenances from the North America mainland.

Sources of variation	df	Expected mean squares	ANOVA for natural populations			ANOVA for provenances		
			S	P > F	VC[1]	MS	P > F	VC[1]
Population or provenance	a-1	$\sigma 2_{,} + n\sigma^2_T + bn\sigma^2_P$	86.9	0.2515	4.3	10.7	0.2828	1.1
Tree	a(b-1)	$\sigma^2_{,} + n\sigma^2_T$	58.8	0.0001	60.1	8.7	0.0001	27.4
Experimental error	a x b(c-1)	$\sigma^2_{,}$	4.9		35.5	3.1		71.6

[1] Percent of the total variance.

Table 2. Spruce cone maggot incidence in natural populations and provenances of white spruce.

Natural population	Average incidence[1]	Provenance identification number[2]	Average incidence
Millertown	19.3a	2451	5.1a
Springdale	12.8a	2444	4.1a b
Badger	11.2a	2459	3.9a b
Glenwood	8.3a	2481	3.6a b
Gambo	7.8a	2463	3.3a b
Norris Arm	6.1a	2475	3.2a b
		2479	3.2a b
		2473	3.1a b
		2472	2.8a b
		2462	2.1a b
		2477	1.7a b
		2483	0.8b

[1] Means expressed as a percent of cones infested with the spruce cone maggot, and compared with Duncan's multiple range test.

[2] See Hall (1986) for origins of North American provenances.

Results and Discussion

There were no significant differences in the incidence of cone maggot among different natural populations ($P = 0.2515$) or among exotic provenances ($P = 0.2828$) of white spruce (Table 1). Only 4% of the total variation in infestation level was attributable to differences among natural populations of white spruce, and 60% of the remaining variation was among trees within populations (Table 1). The low levels of infestation observed in the mainland provenances (Table 2) produced a skewed data set that deviated somewhat from normality ($P > 0.01$). While ANOVA is robust with respect to such deviations, these results must be interpreted with caution. Variation in cone maggot incidence in these provenances demonstrated a pattern similar to that shown in natural populations, with only 4% of the total genetic variation attributable to differences among provenances (Table 1). In Ontario, Turgeon (1990) also reported no significant differences in cone maggot incidence between white spruce clones in seed orchards.

The incidence of cone maggot increased from east to west across Newfoundland. There was a significant difference ($P = 0.0476$) in cone maggot incidence between populations east of Grand Falls (the Gambo, Glenwood, and Norris Arm populations) which had an average cone maggot incidence of 7.4 percent of all cones sampled, and populations west of Grand Falls (the Badger, Millertown, and Springdale populations) which had an average infestation level of 14.2 percent.

The incidence of cone maggot was higher in natural populations (ranging from 6% to 19%), than in the exotic provenances (1% to 5%; Table 2). These preliminary results, based on data from only a single cone crop, suggest that mainland provenances may be less attractive to the cone maggot than local provenances. Local provenances are usually better adapted to local conditions than those from other geographic areas (Namkoong 1969; Zobel and Talbert 1984), although there are exceptions (Namkoong 1969).

The highly significant ($P \leq 0.0001$) tree-to-tree variation in cone maggot incidence observed in both natural populations and among trees within provenances (Table 1) is comparable to observations by Khalil (1974, 1985a), that most of the genetic variation in white spruce is distributed among trees within a stand (or population) as compared with variation among populations or provenances. A similar pattern of significant populations variation occurred within populations for all cone and seed traits measured (Table 3). This pattern of variation indicates that selection for increased tolerance to cone maggot infestation should focus on within population selection. Artificial selection among trees might be useful in natural populations managed for seed production.

Seed losses from cone maggot predation were significant (Tables 3 and 4). An average reduction in number of full seeds/cone of 61% was attributable to maggot infestation, while seed losses attributable to unidentified lepidopterous pests were only about 17% (Table 4). Our observations on seed losses in white spruce due to cone maggot, are similar to the 55% seed losses observed in British Columbia by Hedlin (1973), but somewhat lower than the 75 percent loss reported by Turgeon (1990) for white spruce in Ontario. However, our results cannot account for seed losses due to larvae that died prior to emergence and may underestimate losses due to cone maggot.

A small (4%) but significant ($P > 0.0021$) reduction in the weight of full seeds was observed in cones infested by the cone maggot (Tables 3 and 4). However, a significant interaction ($P = 0.0069$; Table 3) between trees and cone maggot incidence indicates that this reduction in seed weight was inconsistent among trees. Early seedling growth performance in white spruce has been correlated with initial seed weight (Khalil 1981, 1985b), therefore any effect of cone maggot predation on the quality of sound seed remaining within infested cones may be of ecological and commercial significance to forest regeneration efforts.

Cone maggot predation did not have a significant ($P = 0.4722$; Tables 3 and 4) impact on cone weight, suggesting that larval feeding on the cone may be more limited than suggested (Tripp 1952; Hedlin *et al.* 1981). However, significant differences in cone size were reported between healthy and cone maggot infested

Table 3. ANOVA of Cone and seed parameters in natural populations of white spruce.

			No. of full seed/cone		No. of empty seeds/cone		Empty:full seeds/cone		Seed weight		Cone Weight	
Source of Variation	**df**	**Expected mean Squares**	**MS**	**P > F**	**MS**	**P > F**	**MS**	**P > F**	**MS**	**P > F**	**MS**	**P > F**
Population (P)	a-1	$\sigma^2_e + cn\sigma^2_T + bcn\sigma^2_P$	17.5	0.0777	578	0.3000	1.529	0.0146	3.278	0.2443	0.146	0.2843
Tree (T)	a(b-1)	$\sigma^2 + cn\sigma^2_T$	6.8	0.0001	425	0.0001	0.348	0.0001	2.127	0.0001	0.104	0.0001
Damage class (D)	c-1	$\sigma^2_e + n\sigma^2_{TI} + bn\sigma^2_{TI} + abn\sigma^2_I$	63.9	0.0001	16743	0.0001	0.092	0.3114	0.724	0.0021	0.004	0.4722
P x D	(a-1) (c-1)	$\sigma^2_e + n\sigma^2_{TI} + bn\sigma^2_{PI}$	0.3	0.9548	104	0.1926	0.070	0.2480	0.060	0.9560	0.006	0.8989
T x D	(b-1) (c-1)	$\sigma^2_e + n\sigma^2_{TI}$	1.1	0.0599	50	0.5974	0.040	0.1059	0.201	0.0069	0.014	0.0093
Error	abc (n-1)	σ^2_e	0.5		66		0.022		0.066		0.005	

Table 4. Averages for cone and seed traits in white spruce cones classified as healthy, maggot infested or damaged by unidentified insects.

Parameter	Mean ± standard error		
	Healthy	Maggot infested	Miscellaneous
Total no. of seeds/cones	61.2 ± 1.5a	20.8 ± 1.4c	51.2 ± 1.7b
No. of full seeds/cones	19.5 ± 1.0a	7.6 ± 0.8c	16.1 ± 0.9b
No. of empty seeds/cones	41.6 ± 1.2a	13.2 ± 0.8c	35.0 ± 1.2b
Empty:full seeds/cone	2.7 ± 0.2a	2.7 ± 0.3a	2.8 ± 0.2a
1,000 seed weight	2.935 ± 0.054a	2.824 ± 0.064b	2.874 ± 0.054a b
Cone biomass (g)	0.863 ± 0.024a	0.889 ± 0.031a	0.842 ± 0.022a

NOTE: Means compared with Duncan's multiple range test.

white spruce cones by Turgeon (1990) based on observations in seed orchards in Ontario.

Infestation levels of the spruce cone maggot were measured during the bumper cone crop of 1988. This cone crop was the first bumper cone crop in Newfoundland since 1978. Under these conditions, one would expect infestation levels to be relatively low (Mattson 1971). Proportional seed loss due to maggot predation might be much greater during a smaller cone crop. Our study in Newfoundland, and those by Hedlin (1973) in British Columbia, and Turgeon (1990) in Ontario have shown that cone maggot predation can cause serious seed losses, and indicates that special attention should be given to cone maggot populations in seed orchards and seed production areas.

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